Evolutionary Ecology of Sympatric *Catocala* Moths (Lepidoptera: Noctuidae)
III. Experiments on Female Oviposition Preference

Lawrence F. Gall

Entomology Division, Peabody Museum of Natural History, Yale University, New Haven, CT 06511 USA

Abstract. Fecundities and lifespans are documented for 56 species of Nearctic *Catocala* moths, and detailed analysis of oviposition preference is presented for 9 species whose larvae feed on trees in the plant family Juglandaceae. Among these 9 species, 1 restricted oviposition in the field to walnuts (*Juglans*), 1 to pecans (section *§Apocarya* of *Carya*), and 7 to hickories *sensu strictu* (section *§Eucarya* of *Carya*). Shagbark hickory, *Carya ovata*, was greatly preferred by all 7 *Carya* section *§Eucarya* feeders. Large trees were favored over small trees, and there were no temporal differences in timing of oviposition. Oviposition specificity became less crisp as the season progressed and females aged. Patterns in oviposition preference were similar in two geographically distant sites in North America. Laboratory arena tests of preference concorded only modestly well with the field studies, due to the confounding effects of female age, "shagginess" of the oviposition substrate, and arena size.

Introduction

This paper examines the foodplant-linked oviposition biologies of North American *Catocala* Schrank moths, and is the third in a series addressing the evolution of foodplant use in this speciose genus. Fecundity and longevity data are tabulated herein for 56 of the 108 Nearctic *Catocala* species, from all foodplant groups, and more detailed field and laboratory studies of oviposition specificity are presented for 10 of the 25 Juglandaceae-feeding species. Prior papers in this series treat choice and no-choice laboratory foodplant preference tests with *Catocala* larvae (Gall, 1991a), and the distributions of wild larvae on their foodplants (Gall, 1991b).

Materials and Methods
OVIPOSITION ARENA PROTOCOL

An arena design similar to that for larvae (see Gall, 1987, 1991a) was used to assess oviposition preferences of female *Catocala*. Since females of the Juglandaceae-feeding *Catocala* deposit eggs under exfoliating bark and cracks, pieces of bark (ca. 5x15 centimeters) from different trees were used as the food choices. White oak (*Quercus alba* L.) bark was offered as a Type I control choice item (*sensu* Gall, 1991a) in each arena. Females confined to such arenas were fed daily with a honey/syrup solution, diluted by at least one-half to two-thirds with water. Arenas were also frequently sprayed with water to prevent desiccation. Females were generally allowed to live out their lives in arenas, but were

removed when they clearly could no longer make choices among the food items (i.e., legs lost, and/or wings battered).

I used circular plastic containers and small paper bags (ca. 15 cm diam, 15 cm deep) as arenas initially in this work, and subsequently switched to larger paper bags and wire mesh arenas (ca. 30x20x15 cm). Bark samples were taped into the plastic arenas, and sewn into the others. Developing suitable arena designs proved to be a most recalcitrant aspect of these laboratory studies (see below). This stands in contrast to the larval work, in which differing arena geometries and rearing containers had little effect on assays of foodplant preference.

FIELD METHODS FOR STUDYING OVIPOSITION BY WILD FEMALES

Schweitzer (1982) has described the techniques used here to locate ovipositing female *Catocala*. One first carefully scans a trunk of a foodplant tree using a powerful focused-beam search lantern and head lamp. Most ovipositing *Catocala* are readily visible, and sit facing head up on the trunk, with their ovipositors inserted deep into cracks or under shags (some species e.g., *subnata* Grote, tend to oviposit on bark near the base of their foodplants, but most species oviposit from about waist level to 3-5 m up the trunk). After scanning the trunk and major branches, the trunk is then hit several times with a net or stick to flush remaining moths. Many *Catocala* so disturbed from oviposition activity spiral downward, alight, and commence oviposition again on the same tree trunk within a short time. Hitting the trunk thus proved to be a reliable procedure for enticing unreachable females to within net range. Ovipositing female *Catocala* are clearly intent on the task at hand, being largely oblivious to the bright collecting lights and attendant noise when one is searching trees (twig snapping, etc.). This contrasts sharply with their wary behavior at artificial bait sources at night, and flightiness during the daytime.

I conducted several pilot trials using an infra-red "sniper scope" to observe female *Catocala*, but abandoned this method early on in favor of lanterns and head lamps, for simplicity. Doubtless such infra-red viewing devices would prove useful in examining the oviposition behavior of other night-flying Lepidoptera that are disturbed by light in the visible spectral range.

DESCRIPTIONS OF STUDY SITES

Searches for ovipositing *Catocala* were carried out from 1980-1987 at four localities in Connecticut and Tennessee (USA). Three of the Connecticut sites were in New Haven County: West Rock, Brooksvale Park (Hamden), and Southbury; the other, West Redding, was in Fairfield County. Data from the Connecticut localities were recorded separately, but are pooled here for analysis as the biological patterns proved consonant among sites. The Tennessee searches were conducted during 1985 and 1986 at Celina (Clay County), a locality with a rich Juglandaceae-feeding *Catocala* fauna (Miller, 1977), and where many of the more southerly species replace or are numerically commoner than those present in Connecticut.

The collecting routes were all selected to include a representative array of available juglandaceous foodplants. At West Rock, West Redding, and Celina the routes were largely woodland paths; at Brooksvale Park and Southbury, the routes were woodland margins. However, the routes at each locality included both types of habitat. Small to medium (ca. 5-15 cm dbh) hickories and walnuts

predominated at West Rock, while large (>25 cm dbh) trees occured at the other habitats. Shagbark hickory, *Carya ovata* Mill. K. Koch of section *§Eucarya* DC., was the most prevalent hickory at all sites, although West Rock had a substantially larger number of pignut hickory (*C. glabra* Mill. Sweet of section *§Eucarya*) than did the other localities. Shellbark hickory (*C. laciniosa* Michx. Loud. of section *§Eucarya*) occured only at Celina, and this locality was the only one lacking butternut (*Juglans cinerea* L.).

TREE AND MOTH PARAMETERS

For each tree surveyed, I recorded the collecting locality and species identity. For most I also recorded size as: small (5-10 cm dbh), medium (10-20 cm dbh) or large (>20 cm dbh). The majority of trees sampled greatly exceeded 20 cm dbh, except at West Rock. I recorded the species identity of each moth, but did not index age because of lack of mark-recapture data on *Catocala* with which one would calibrate age. Only those moths which were positively identifiable to species, and whose ovipositors were clearly inserted into bark crevices were scored as ovipositing (these were the vast majority of all observations). At each locality, I worked a predefined collecting route. I usually repeated the route twice (occasionally three or four times) per night. Since moths were removed from trees each time, and at least 30-45 minutes separated repeat checks, I treated all tree samples as independent observations. Most sampling was conducted between 0830 and 1130 hours. Statistical testing follows Gall (1991a).

Results
LABORATORY STUDIES
1. LONGEVITY AND FECUNDITY OF FEMALE *CATOCALA*

Table 1 presents longevity (in days) and fecundity data for 56 *Catocala* species that I have confined over the years for arena tests or for securing eggs for subsequent rearing (information is presented only for those moths that did in fact lay eggs, which was the great majority of all females). Few of the moths whose data are shown were freshly eclosed when captured. Thus, the Table 1 data must be considered minimum estimates of longevities and fecundities of wild *Catocala* females. In addition, Table 1 is somewhat biased toward more mature female moths, since newly eclosed females often will refuse to lay and/or will produce infertile eggs, and my primary reason for confining female *Catocala* always was to obtain breeding/experimental stock for the subsequent larval field season.

Considering all 56 species, there were significant positive correlations between longevity and moth size (Spearman rank: $r=+0.22$, $n=211$, $p<.01$), and fecundity and moth size ($r=+0.45$, $n=253$, $p<.01$; size indexed by forewing length taken from species accounts in Sargent, 1976). Within each of the six foodplant groups represented here by more than one taxon, the correlations between longevity-size and fecundity-size were again positive, but none of the correlations was significant. There were no significant differences in longevity as a function of foodplant group, but fecundities of females in the Salicaceae, Juglandaceae, and Myricaceae groups tended to be greater than fecundities of females in the

Table 1. Longevities and fecundities of female *Catocala* in oviposition containers (arenas and otherwise). Means, maxima, and sample sizes indicated for both parameters. Means by foodplant family given below main Table; families connected by the same vertical bar are not significantly different at the 0.05 level (Tukey HSD tests). Egg size gives mean maximal diameter and mean maximal vertical height of sample of 10 eggs, rounded to the nearest 5 micrometer units (scale: 50 micrometer units per mm).

Species	Egg Size diameter	height	Number Eggs Laid mean	n	max	Lifespan mean	n	max	Foodplant Family
andromedae	50	30	53.2	6	159	13.4	5	19	Ericaceae
gracilis	50	30	32.3	3	68	16.0	2	26	Ericaceae
louisae	45	30	20.5	2	21	9.0	1	9	Ericaceae
sordida	50	30	30.5	6	57	10.3	3	13	Ericaceae
amica	45	20	46.0	3	72	16.5	2	18	Fagaceae
coccinata	70	30	77.2	6	116	11.5	4	14	Fagaceae
connubialis	50	20	54.8	4	120	11.0	3	13	Fagaceae
herodias	65	40	118.4	5	198	16.0	2	20	Fagaceae
ilia	70	40	122.3	7	312	14.6	5	19	Fagaceae
lineella	45	20	89.2	5	150	18.7	3	21	Fagaceae
micronympha	55	20	53.8	4	104	8.8	4	17	Fagaceae
similis	50	20	52.1	7	109	12.3	3	18	Fagaceae
angusi	50	20	463.5	4	1493	31.8	4	35	Juglandaceae
consors	40	30	123.0	2	151	.	.	.	Juglandaceae
dejecta	65	20	219.5	2	258	23.5	2	28	Juglandaceae
epione	55	45	85.6	5	136	11.4	5	18	Juglandaceae
flebilis	50	20	44.0	5	109	21.0	5	42	Juglandaceae
habilis	45	20	100.3	4	248	28.3	3	38	Juglandaceae
insolabilis	60	20	61.8	4	190	10.0	5	15	Juglandaceae
judith	50	20	59.3	4	169	13.3	3	25	Juglandaceae
lacrymosa	55	20	169.3	7	381	25.4	7	40	Juglandaceae
luctuosa	50	20	304.0	1	304	26.0	1	26	Juglandaceae
maestosa	50	20	224.5	2	388	18.0	2	20	Juglandaceae
nebulosa	55	25	58.2	5	153	22.8	4	29	Juglandaceae
neogama	55	20	377.8	4	1102	21.5	6	32	Juglandaceae
obscura	55	20	291.5	11	621	21.4	9	39	Juglandaceae
palaeogama	55	20	317.9	14	694	22.9	12	52	Juglandaceae
piatrix	50	25	164.0	5	400	14.0	2	20	Juglandaceae
residua	55	20	352.7	3	480	26.3	6	37	Juglandaceae
retecta	55	20	277.0	14	625	18.7	13	41	Juglandaceae
robinsoni	45	20	46.0	1	46	41.0	1	41	Juglandaceae
serena	50	20	72.0	1	72	38.0	1	38	Juglandaceae
subnata	60	25	237.3	4	506	12.3	4	15	Juglandaceae
ulalume	50	20	44.0	1	44	9.0	1	9	Juglandaceae
vidua	50	20	104.5	2	165	.	.	.	Juglandaceae
innubens	50	35	59.5	4	150	11.0	3	19	Leguminoseae
antinympha	45	30	98.5	4	226	13.5	2	15	Myricaceae
badia	45	30	96.0	4	150	10.5	2	15	Myricaceae
coelebs	50	30	171.7	3	405	.	.	.	Myricaceae
muliercula	40	30	248.0	2	270	18.0	2	22	Myricaceae

Species	Egg Size diameter	height	Number Eggs Laid mean	n	max	Lifespan mean	n	max	Foodplant Family
blandula	55	20	29.2	5	49	10.0	4	14	Rosaceae
crataegi	50	20	80.0	3	92	13.5	2	16	Rosaceae
grynea	50	20	62.6	5	99	15.3	7	27	Rosaceae
mira	55	20	49.6	7	79	9.2	6	17	Rosaceae
praeclara	50	20	57.5	13	278	14.8	6	34	Rosaceae
pretiosa	55	20	31.1	7	72	13.5	10	19	Rosaceae
ultronia	55	20	84.4	7	193	17.3	7	24	Rosaceae
amatrix	45	35	452.0	2	600	20.0	3	32	Salicaceae
briseis	60	35	74.5	2	99	.	.	.	Salicaceae
cara	50	35	286.7	3	538	15.9	9	27	Salicaceae
carissima	45	30	42.0	1	42	63.0	1	63	Salicaceae
concumbens	55	40	157.8	5	241	15.5	4	21	Salicaceae
parta	55	35	112.0	2	174	25.0	1	25	Salicaceae
relicta	60	45	153.3	4	202	11.8	4	25	Salicaceae
unijuga	65	40	75.0	2	100	35.5	2	37	Salicaceae
cerogama	45	35	73.5	2	107	10.0	3	14	Tiliaceae
Means:			214.7			20.9			Juglandaceae
			177.7			19.6			Salicaceae
			137.6			14.0			Myricaceae
			80.4			13.3			Fagaceae
			55.4			13.7			Rosaceae
			37.7			12.6			Ericaceae

Fagaceae, Rosaceae, and Ericaceae groups (see Table 1). Note that
nearly all of the Salicaceae, Juglandaceae, and Myricacae feeding species
in Table 1 are larger than the corresponding Fagaceae, Rosaceae, and
Ericaceae feeders.

2. ARENA TESTS

Table 2 gives the results of 20 arena experiments with Juglandaceae
feeders. In 11 of the arenas, oviposition on either the Type I control
Quercus alba and/or the arena itself (noted in Table 2 as "Fraction
Haphazard") accounted for nearly 20 percent or more of all eggs laid.
Using wire mesh cages greatly reduced oviposition on the arenas them-
selves, but nevertheless did not curb oviposition on the Type I control.

Haphazard laboratory oviposition on plants not in the preferred
foodplant family is squarely at odds with field oviposition results with
these same moth species (see below under Results and Discussion). I
therefore consider only 9 of the 20 arenas to be "successful," these being
starred in Table 2 and characterized by less than five percent of all eggs
being laid on arenas and Type I controls (the *piatrix* Grote and *subnata*
arenas are considered successful despite ca. 10 percent hapazard ovipo-
sition, since the numbers of misplaced eggs were very low).

Of the seven successful arenas with *Carya* feeders, five are for
palaeogama Guenee, and single females represent each of *residua*

Table 2. Oviposition arena results with Juglandaceae-feeding *Catocala*. Values in Table are percents of eggs laid on choice items. "Successful" arenas starred. See text for elaboration.

Catocala feeding on section §*Eucarya* of *Carya*

Species-Brood	Carya ovata	Carya glabra	Carya tomentosa	Quercus control	Arena	Total Ova	Fraction Haphazard	Arena Style	Start Date
obscura-A80	21.1	35.4	3.7	0.2	39.5	488	39.7	plastic	31 Aug
obscura-B80	36.4	35.2	1.4	12.4	14.5	621	26.9	bag	28 Aug
obscura-A81	19.0	60.3	0.7	20.1	0.0	448	20.1	wire	17 Aug
obscura-B81	1.4	79.6	1.0	18.0	0.0	289	18.0	wire	24 Aug
obscura-C81	6.4	0.0	0.0	93.6	0.0	31	93.6	wire	28 Aug
* palaeogama-A80	24.8	62.9	10.4	0.0	2.0	694	2.0	plastic	26 Aug
* palaeogama-B80	42.6	41.8	12.4	3.2	0.0	251	3.2	plastic	27 Aug
* palaeogama-C80	15.8	64.5	19.7	0.0	0.0	183	0.0	plastic	26 Aug
palaeogama-D80	1.2	10.1	28.3	12.2	48.2	647	60.4	bag	27 Aug
* palaeogama-B81	42.0	52.0	1.4	4.5	0.0	440	4.5	wire	18 Aug
palaeogama-C81	7.9	21.2	0.0	70.9	0.0	203	70.9	wire	29 Aug
* palaeogama-D81	34.4	65.6	0.0	0.0	0.0	282	0.0	wire	27 Aug
* residua-B80	56.0	40.0	2.7	0.0	1.2	480	1.2	bag	26 Aug
retecta-C80	22.1	34.5	12.6	1.3	29.4	625	30.7	bag	28 Aug
retecta-A81	33.3	37.2	1.5	28.0	0.0	457	28.0	wire	24 Sep
retecta-B81	13.0	60.2	4.2	22.7	0.0	216	22.7	wire	18 Aug
* retecta-D81	49.1	29.6	19.5	1.8	0.0	169	1.8	wire	24 Aug

Catocala feeding on *Juglans* and/or section §*Apocarya* of *Carya*

Species-Brood	Carya ovata	Juglans nigra	Carya cordiformis	Quercus control	Arena	Total Ova	Fraction Haphazard	Arena Style	Start Date
neogama-X80	10.5	36.7	0.0	24.5	28.3	1102	52.8	plastic	28 Aug
* piatrix-A81	7.5	70.0	10.0	12.5	0.0	40	12.5	wire	18 Aug
* subnata-B81	5.3	26.4	57.9	10.5	0.0	19	10.5	wire	27 Aug

Strecker and *retecta* Grote. In all seven arenas, *Carya ovata* and *C. glabra* were prefered over *C. tomentosa* Nutt. (p<.05 by ANOVA for *palaeogama*; G=296.18, df=2, p<.01 for *residua*; G=96.75, df=2, p<.01 for *retecta*). In the remaining 2 arenas, the *Juglans*-feeding *piatrix* preferred *Juglans* (G=31.71, df=2, p<.01), and the *Carya*-feeding *subnata* likewise preferred *C. cordiformis* (Wang.) K. Koch of section *§Apocarya* DC. (G=9.50, df=2, p<.05).

FIELD STUDIES
1. Tree Distributions
I surveyed a total of 1552 hickories and walnuts for *Catocala* from 1980 through 1987. Table 3 gives relevant summaries of the trees at each locality, and breaks down the Connecticut trees as a function of size. Since the same routes were repeated each year, there was by definition no year to year variation in the relative frequencies of juglandaceous foodplants sampled at each locality. Although an unbiased analysis of tree size is precluded by repeat sampling of the same trees each year, tree size clearly differed as a function of tree species (G=38.02, df=10, p<.01, treating repeats as independent).

2. Oviposition as a Function of Foodplant Genus
I recorded 259 ovipositing female *Catocala* from these 1552 trees (Table 4). A total of 10 females were noted ovipositing on *Juglans*, 13 on *Carya cordiformis* of section *§Apocarya*, and 236 on *Carya* of section *§Eucarya*.

Females of *subnata* oviposited in Connecticut on *C. cordiformis* (one observation also on *Juglans cinerea*; *subnata* is rare at the Celina,

Table 3. Numbers of juglandaceous trees searched for ovipositing female *Catocala*. Above, by state; below, tree size distributions for Connecticut localities.

State:	Carya ovata	Carya glabra	Carya tomentosa	Carya laciniosa	Carya cordiformis	Juglans cinerea	Juglans nigra	Total
Connecticut	640	361	68	.	184	66	39	1358
Tennessee	97	36	4	26	6	.	25	194
Total	737	397	72	26	190	66	64	1552

Tree Size:	Carya ovata	Carya glabra	Carya tomentosa	Carya laciniosa	Carya cordiformis	Juglans cinerea	Juglans nigra	Total
Large	383	181	27	.	120	41	18	770
Medium	137	115	25	.	32	10	4	323
Small	71	35	13	.	26	10	2	157
Total	591	331	65	.	178	61	24	1250

Table 4. Field oviposition records for female Juglandaceae-feeding *Catocala*, by state and tree species. P = significance level for preference of favored foodplant genus versus all other juglandaceous foods (G-tests or exact multinomial probabilities).

Connecticut	*Carya ovata*	*Carya glabra*	*Carya tomentosa*	*Carya laciniosa*	*Carya cordiformis*	*Juglans cinerea*	*Juglans nigra*	Total	Favored Foodplant	p
judith	8	0	0	.	0	0	0	8	*Carya* sect. *§Eucarya*	.29
obscura	31	0	0	.	0	0	0	31	*Carya* sect. *§Eucarya*	< .01
palaeogama	84	17	7	.	1	0	0	109	*Carya* sect. *§Eucarya*	< .01
residua	34	1	0	.	0	0	0	35	*Carya* sect. *§Eucarya*	< .01
retecta	13	2	0	.	0	0	0	15	*Carya* sect. *§Eucarya*	.06
subnata	0	0	0	.	12	1	0	13	*Carya* sect. *§Apocarya*	< .01
neogama	0	0	0	.	0	5	2	7	*Juglans*	< .01
Total	170	20	7	.	13	6	2	218		

Tennessee	*Carya ovata*	*Carya glabra*	*Carya tomentosa*	*Carya laciniosa*	*Carya cordiformis*	*Juglans cinerea*	*Juglans nigra*	Total	Favored Foodplant	p
flebilis	2	0	0	0	0	.	0	2	*Carya* sect. *§Eucarya*	.
obscura	8	0	0	0	0	.	0	8	*Carya* sect. *§Eucarya*	.49
palaeogama	11	1	0	1	0	.	0	13	*Carya* sect. *§Eucarya*	.21
residua	15	0	0	0	0	.	0	15	*Carya* sect. *§Eucarya*	.15
serena	1	0	0	0	0	.	0	1	*Carya* sect. *§Eucarya*	.
neogama	0	0	0	0	0	.	2	2	*Juglans*	< .05
Total	37	1	0	1	0	.	2	41		

Tennessee locality). Females of *neogama* Smith oviposited on *Juglans* in both Connecticut and Tennessee. Females of *flebilis* Grote, *judith* Strecker, *obscura* Strecker, *palaeogama*, *residua*, *serena* Edwards, and *retecta* all oviposited on *Carya* in both Connecticut and Tennessee. No ovipositing female *nebulosa* Edwards were observed in Tennessee, though I collected the species commonly there at lights and on tree trunks during the daytime.

In Connecticut, *C. ovata* was significantly preferred over other *Carya* by *judith*, *obscura*, *palaeogama*, and *residua* (p<.05 for each *Catocala*, exact binomial probabilities; p=0.053 for *retecta*). Females of *obscura*, *palaeogama*, and *residua* preferred to oviposit on large trees (p<.05 for each as above, test is large trees versus all others; for *judith*, p=.091). In Tennessee, *C. ovata* was similarly preferred by *obscura* and *residua* (p<.05 for each as above; for *palaeogama*, p=.103). There were too few observations to draw firm conclusions about oviposition specificity in *flebilis* and *serena*.

No *Catocala* species showed differences in oviposition preference as a function of year (p>.25 in each case by G-tests, controlling for state). Two Connecticut ovipositions represent what I consider to be "mistakes" — a *palaeogama* ovipositing on *C. cordiformis*, and a *subnata* on *Juglans cinerea*. These two observations are discussed later in the context of female moth age.

3. TEMPORAL PATTERNS

Table 5 presents the mean time of night for oviposition by the seven Connecticut Juglandaceae-feeding *Catocala* species. There were no differences in timing of oviposition among any of these species (p>.15 by ANOVA considering all, p>.25 for just the *Carya* feeders). Curiously, I found no ovipositing *habilis* Grote in this study, although adults were generally common at bait and light on the same nights in both Connecticut and Tennessee. Since my tree searches ended prior to midnight, it may be that this species oviposits principally late at night. Late night to pre-dawn flight characterizes a number of other *Catocala*, such as the oak-feeding *herodias* Strecker (personal observations of myself, D. Hawks, and D. Schweitzer). Sampling was conducted rather late in each season to expect *epione* Drury (adults fly in late June and early July in Southern Connecticut), and I suspect from other work with *epione* females, and the distribution of its young larvae in the field (Gall,

Table 5. Mean time of night (EST) for oviposition by wild female Juglandaceae-feeding *Catocala* in Connecticut. All species oviposit at similar times.

| Species | Time of Oviposition | | |
	Mean	SD	N
judith	20:56	00:31	4
subnata	21:01	00:28	11
palaeogama	21:09	00:36	88
residua	21:10	00:22	22
obscura	21:13	00:43	23
retecta	21:15	00:35	12
neogama	21:50	00:34	6

Table 6. Mean numbers of ovipositing female Juglandaceae-feeding *Catocala* per tree in Connecticut, as a function of year and foodplant species. Note decline in numbers from 1980 through 1984 on all tree species.

Species	Number of Females Per Foodplant Tree					
	1980	1981	1982	1983	1984	1987
Carya glabra	0.12	0.03	0.00	0.00	0.00	0.00
Carya ovata	0.45	0.20	0.00	0.02	0.36	0.25
Carya tomentosa	0.22	0.04	0.00	0.00	0.00	0.00
Carya cordiformis	0.15	0.04	0.00	0.00	0.06	0.00
Juglans sp.	0.31	0.08	0.00	0.00	0.00	0.00
Total Trees Surveyed	371	674	125	55	87	46

1991b) that this species oviposits on small trees, near the base of the trunk.

4. Moth Densities on Foodplants

The mean number of ovipositing females per tree is presented in Table 6, by foodplant and year. As with the larval field data for the same *Catocala* species (Gall, 1991b), these oviposition records reflect the sharp drop in adult *Catocala* numbers at light trap samples in Connecticut during 1980-1984. The decline in female abundance from 1980-1984 in Table 6 is highly significant for each foodplant genus ($p < .01$ by G-tests, trees split each year into two classes: having no females, having one or more female).

Table 7 shows plots of the number of ovipositing *palaeogama*, *residua*, and *obscura* per *C. ovata* in Connecticut and Tennessee, for years when moth abundance was high. The variance to mean ratios are not substantially greater than one, no distribution being significantly different from poisson (i.e., random; $p > .25$ for each by exact binomial tests). Stated another way, ovipositing females of the same species did not congregate on individual *C. ovata* trees (compare these distributions to those for larvae of the same *Catocala* species in Gall, 1991b).

Table 7 also shows similar plots of the number of all ovipositing *Catocala* per tree. Again, the variance to mean ratios showed no clear trends, and the distributions were similarly random ($p > .25$ in each). Thus, there was no tendency for ovipositing *Catocala* females on the whole to congregate on individual *C. ovata* or *C. glabra* trees. The pattern was the same for the other *Carya* foodplants, for which far fewer observations were available (virtually all records being of single ovipositing *Catocala*, or none). Therefore, it appears that individual *Catocala* females select suitable oviposition sites without regard to the presence or absence of other females. Since there is a superabundance of such sites

Table 7. Numbers of ovipositing female Juglandaceae-feeding *Catocala* per individual tree: by year, *Catocala* species, collection locality, and foodplant species. Variance to mean ratios for all distributions are near 1.0, indicating no clumping of females on trees (no distribution is significantly different from random i.e., Poisson at the 0.05 level; G-tests or exact multinomial probabilities).

| Species | State | Year | Foodplant | Number of Moths | | | | | Totals | | Moths/Tree | |
				0	1	2	3	>3	Moths	Trees	Mean	Var/ Mean
obscura	CT	1980	*Carya ovata*	80	11	2	1	0	18	94	0.19	1.38
obscura	CT	1981	*Carya ovata*	247	8	1	0	0	10	256	0.04	1.16
palaeogama	CT	1980	*Carya glabra*	96	9	1	0	0	11	106	0.10	1.09
palaeogama	CT	1980	*Carya ovata*	70	19	3	2	0	31	94	0.33	1.26
palaeogama	CT	1981	*Carya ovata*	235	19	1	0	0	21	256	0.08	1.01
palaeogama	CT	1984	*Carya ovata*	44	7	2	0	0	11	53	0.21	1.18
palaeogama	TN	1986	*Carya ovata*	48	5	1	0	0	7	54	0.13	1.18
residua	CT	1980	*Carya ovata*	85	8	1	0	0	10	94	0.11	1.11
residua	CT	1981	*Carya ovata*	240	15	1	0	0	17	256	0.07	1.06
residua	TN	1986	*Carya ovata*	45	8	1	0	0	10	54	0.19	1.03
all taxa	CT	1980	*Carya glabra*	93	12	1	0	0	13	106	0.13	1.02
all taxa	CT	1980	*Carya ovata*	50	30	8	3	3	67	94	0.71	1.35
all taxa	CT	1981	*Carya ovata*	207	40	7	2	0	60	256	0.23	1.20
all taxa	CT	1984	*Carya ovata*	39	9	5	0	0	19	53	0.36	1.19
all taxa	TN	1986	*Carya ovata*	35	15	4	0	0	23	54	0.43	0.94

on individual *C. ovata* trees, and eggs are placed far into crevices, it is doubtful that females assess egg load on trees before ovipositing (I regularly find eggs and eggshells of several *Catocala* species under the same piece of exfoliating bark).

Implicit in the above analyses is that the spatial distribution of these hickories was not strongly contagious, a pattern which by itself could confound interpretation of moth densities on trees, as well as influence conclusions about female preferences among different foodplants species. Both intraspecific and interspecific distributions of the foodplant trees are relevant (Courtney and Courtney, 1982, for the former; Stanton, 1982, for the latter). At the Connecticut localities of Brooksvale Park, Southbury, and West Redding, farming and landscaping practices have generated an approximately regular distribution of all hickories. Large trees (often hickory and maple) are planted, or culled, at intervals along the edges of fields. This reduces the possibility of "edge-effects" within monotypic clumps of trees, but probably does not greatly affect interspecific tree clumping. At West Rock and Celina, where neither farming nor landscaping is now manifest, there may be some tendency for small trees to be clumped (both intra- and interspecific stands), but medium sized and large trees are encountered only sporadically.

Discussion

GENERAL TRENDS IN OVIPOSITION SPECIFICITY

The field studies presented above show that ovipositing female Juglandaceae-feeding *Catocala* discriminate among the three major taxonomic divisions within Juglandaceae: *neogama* oviposits on *Juglans*; *subnata* on *Carya* section *§Apocarya*; and *judith, obscura, palaeogama, residua*, and *retecta* on *Carya* section *§Eucarya*. Within *Carya* section *§Eucarya*, shagbark hickory (*C. ovata*) is always preferred over other hickories. In both Connecticut and Tennessee, two geographically distant sites with differing juglandaceous floras, oviposition preferences by wild female *Catocala* are quite close even down to the foodplant species level.

Oviposition by both *flebilis* and *serena*, represented here by small sample sizes, will likely also prove to be restricted to *Carya* (the few other recorded ovipositions for *serena* are all *C. ovata*; Nielsen, 1978, and in litt.). Field data on *nebulosa* are presently lacking, but I have determined a wild egg collected in Michigan on *Carya cordiformis* by M. Nielsen to be *nebulosa* (confirmation by scanning electron microscopy; the egg SEM profiles of nearly all Nearctic *Catocala* are now known), and its larvae only ate *Carya* section *§Apocarya* in foodplant preference tests (Gall, 1991a). Thus, it seems probable that *nebulosa* will prove to limit oviposition to *Carya* section *§Apocarya*, as does *subnata*.

In contrast to my field studies with Juglandaceae-feeding *Catocala* larvae (Gall, 1991a, 1991b), I did not systematically sample non-juglandaceous trees at the same time for ovipositing females, to allow explicit tests of foodplant family level oviposition specificity. However, I have certainly examined well in excess of 300 trees (most of which were oaks) in other *Catocala* foodplant groups during the course of these nightly walks, and never noted an ovipositing Juglandaceae-feeding *Catocala* on these other foodplant trees. Additionally, during studies of oviposition by Rosaceae-feeding *Catocala*, Schweitzer (1987, and in litt.) has similarly failed to record other than Rosaceae feeders on those plant arrays. Thus, there is little question that the Juglandaceae-feeding *Catocala* discussed here oviposit solely on juglandaceous foodplants.

Note that Rowley & Berry (1912) did report finding eggs of the oak-feeding *ilia* Cramer very rarely on *C. ovata* in Missouri. I have taken only one *ilia* egg under a *C. ovata* shag (in Connecticut in 1984, among numerous shags examined for eggs and hatched egg shells over the years), and Schweitzer (1982) obtained exclusively Juglandaceae-feeding *Catocala* (over 100 individuals representing 4 species) from 18 *C. ovata* whose egg faunas he surveyed by placing shags into rearing sleeves in early spring.

OVIPOSITION SPECIFICITY VS. LARVAL FOODPLANT USE

Whether female oviposition choice and larval feeding biologies agree is of interest to studies of the evolutionary history of foodplant ecology in

the genus *Catocala*. For the species treated in this paper, such concordances appear to be absolute at the foodplant family level, with all 10 Juglandaceae-feeding *Catocala* ovipositing solely on Juglandaceae in the field, their first instars preferring only these same plants in arena tests (Figures 1-3 in Gall, 1991a), and the wild larvae being found only on these same plants (Table 3 in Gall, 1991b). The concordances appear nearly as absolute within Juglandaceae, with one taxon (*neogama*) ovipositing and feeding as larvae in both lab and field on *Juglans*, one on *Carya* section *§Apocarya* (*subnata*), and five on *Carya* section *§Euearya* (*judith*, *obscura*, *palaeogama*, *residua*, *retecta*). Furthermore, for each of these seven *Catocala* species, larval growth and survival are also uniformly best on the foodplants preferred by wild females for oviposition (Table 4 in Gall, 1991a).

Only the laboratory oviposition specificity tests do not agree closely with the larval feeding biologies. Most of the disagreement seems traceable to the confounding influences of female age and bark sample "shagginess" (see below), as the few successful oviposition arenas with *palaeogama*, *piatrix*, *residua*, *retecta*, and *subnata* do match larval feeding patterns moderately well at the foodplant genus level. Among the southern Connecticut *Carya*-feeding *Catocala*, there is some variability in the otherwise precise correspondences between wild female oviposition and larval foodplant specificities, but only for *palaeogama* and *retecta*, the two most oligophagous of the taxa (*habilis*, *judith*, *obscura*, and *residua* are all specialists linked tightly to the biology of *C. ovata*). For 1 *retecta* and 3 *palaeogama* broods, data are available on the foodplant preferences of the females and their larval progeny (cf. Table 2 above; and Table 4 in Gall, 1991a).

The mother of *retecta* brood E81 was collected as she oviposited on *C. ovata*. She was not tested in an oviposition arena, and her progeny ate much more *C. glabra* in first instar arenas than other food choices. Survival and growth rate of her larvae were but slightly higher on *C. ovata* than on *C. glabra*. The mother of *palaeogama* brood A80 was collected while she oviposited on *C. ovata*. In oviposition arenas, she laid more eggs on *C. glabra* than on *C. ovata*. Her progeny overwhelmingly preferred *C. ovata* to other *Carya* in first instar arena tests, and similarly developed fastest on *C. ovata* in no-choice sleeve rearings. The mother of *palaeogama* D80 was taken while she oviposited on *C. tomentosa*. She laid most of her eggs on the arena (a paper bag) rather than on bark samples. Her progeny ate equal amounts of *C. ovata* and *C. tomentosa*, but they were not reared in sleeve experiments. The mother of *palaeogama* brood E80 was taken while she oviposited on *C. glabra*. She was not tested in an arena, and her first instars preferred *C. ovata* two to one over *C. tomentosa*, and ate virtually no *C. glabra*. Her larvae developed most rapidly on *C. ovata* in sleeve rearings.

The only consistent pattern to emerge from the foregoing comparisons is that *C. ovata* seems to best support larval growth, irrespective of

female oviposition history. There is no indication that pronounced "host races" are developed at present in the hickory-feeding *Catocala* who regularly use *Carya* other than the universally preferred *C. ovata*. However, I suspect that local or larger-scale host races may prove to be common among the Rosaceae-feeding *Catocala* when their field biologies are examined closely (my unpublished rearing data).

THE OVIPOSITION ARENA FAILURES: THE EFFECT OF FEMALE AGE

Limitations in arena methodology are suggested by the failure of most captive females to discriminate against the arena walls and, especially, the Type I control (white oak, *Quercus alba*) — on which oviposition by the same *Catocala* species does not occur in the field. First, the flight space offered in these arenas is relatively small compared to the wingspan of most *Catocala*. Second, volatile olfactory cues that might be used by *Catocala* to identify foodplants will mix in plastic and paper arenas closed to strong ventilation (the wire mesh arenas were well ventilated), and when coupled with small arena size, this could easily occlude cues which guide female choice. The exclusive use of wire mesh arenas in 1981 reduced the problem of oviposition on arena walls, but the females continued to oviposit heavily on the Type I control, *Quercus alba*.

Two uncontrolled intervening variables seem relevant to this persistent tendency of females to oviposit on *Quercus alba* in arenas: female age, and the "shagginess" of bark samples. Both variables need to be explored further, but low adult *Catocala* numbers in New England since 1981 (and the more pressing need to secure adequate rearing stocks each summer from the few captured females) have limited efforts to design follow-up arena tests.

For the *Carya*-feeding species listed in Table 2, there is a positive correlation between the date a female was confined to her arena and the fraction of eggs she placed "haphazardly" on arena walls and Type I controls. The trend is significant for the 1980 arenas (Spearman rank r=+0.78, n=8, p<.05), but not so for 1981, although it is positive (r=+0.31, n=9, p>.25). Table 8 shows 1981 Connecticut ovipositions for *palaeogama* (the most abundant species in the best year), on *C. ovata* versus all other foodplants, as a function of sampling date. The percentage of ovipositions on trees other than *Carya ovata* increases as the season progresses (Spearman rank r=+0.98, n=6, p<.05; more conservative pooling strategies for sampling date do not eliminate the significance). Schwarz (1923), working with caged *Catocala cara* females, noted a comparable increase in ovipositions on other than the preferred foodplant (willow) as the females aged (his data are summarized in Table 9).

In addition, the only Connecticut *residua* (n=1) and *retecta* (n=2) ovipositions on *Carya* other than *C. ovata* were similarly late in the 1980 season (27 August, 30 August, and 1 September, respectively). Moreover, the two "mistakes" noted earlier in the Results were also late in the

Table 8. Oviposition by wild *Catocala palaeogama* females in Connecticut during 1981, by date and foodplant species. Preference for oviposition on *Carya ovata* breaks down as the season progresses and females age.

| | Number of Ovipositions | | | | | |
	July Week 4	August Week 1	August Week 2	August Week 3	August Week 4	September Week 1
Carya ovata	5	4	10	4	3	0
another tree	0	0	1	2	2	1

Table 9. Oviposition by caged *Catocala cara* females, by date and foodplant species. Preference for oviposition on willow breaks down as females age. Data from Schwarz (1923).

Number of Ovipositions	August 19	August 20	September 15	September 16
Female 1				
willow	10	21	0	0
poplar	0	0	2	1
hickory	0	0	0	2
Female 2				
willow	11	30	0	0
poplar	0	0	0	0
hickory	0	0	0	1

season: a *palaeogama* on *Carya cordiformis*, 29 August 1981; a *subnata* on *Juglans cinerea*, 28 August 1980.

These several lines of evidence indicate that oviposition specificity broadens as females grow older (although adult *Catocala* typically live for several weeks or more, and pupal eclosion in the field is no doubt spread over at least a 1-2 week period, it is certainly safe to state that the average age of females in late August and September is greater than in late July and early to mid August). The broadening in oviposition specificity is likely in part a simple correlate of deteriorating sensory capacity. However, it may also in part be an adaptive response to aging, as somatic reserves are depleted and fecundity and fertility decline (sharpest discrimination might be favored selectively in younger females: larvae hatching from these earlier eggs would likely be better nutritionally provisioned than those from late eggs, and perhaps be at a competitive advantage, both intra- and interspecifically). Thus, older females might be viewed as having more freedom to experiment with secondarily suitable foodplants (e.g., trees other than *C. ovata* for the *Carya*-feeders), with less risk of compromising already successful reproductive effort.

THE OVIPOSITION ARENA FAILURES: THE EFFECT OF BARK SHAGGINESS

The roughness of bark samples also seems responsible in part for the unusual haphazard oviposition by captive Juglandaceae-feeding *Catocala* in arenas. Bark of the Type I arena controls, white oak (*Quercus alba*), is rough, like that of *Carya ovata* and *C. glabra*, and exfoliates slightly (as in only *C. ovata*). Only the bark of *C. tomentosa* is smooth (in contrast to *C. ovata*, *C. glabra*, and *Quercus alba*), and even massive *C. tomentosa* have roughened bark largely only near their bases.

In all arenas with *Carya* feeders, fewer eggs were laid on the non-shaggy *C. tomentosa* than on the other *Carya* species ($p<.05$ by ANOVA, successful and unsuccessful arenas combined). Likewise, fewer eggs were laid on *C. tomentosa* than on *Quercus alba* plus arena crevices ($t=20$, $n=16$, $p<.01$ by Wilcoxon test; $t=3$, $n=8$, $p<.05$ for same test using 1981 arenas only, in which the use of wire mesh cages eliminated oviposition on arenas). Lastly, 3 of the 4 arenas in which more eggs were laid on *C. tomentosa* than on the oak/arena were with *palaeogama* confined in plastic containers, in which no crevices or seams were present.

Thus, the shagginess of an oviposition substrate seems also to be important to ovipositing *Catocala*, along with foodplant species. In this context, consider too that the genital morphology of female *Catocala* is clearly geared toward concealing eggs in inaccessible places such as shags, crevices and cracks: the ovipositor is strongly dorso-laterally flattened, secondarily sclerotized, and highly extensible; and the eggs of most of the Juglandaceae feeders, the Nearctic Rosaceae feeders, and some of the Nearctic oak feeders are also dorso-laterally flattened, in contrast to the usual hemispherical *Catocala* egg.

Literature Cited

COURTNEY, S.P., and S. COURTNEY. 1982. The 'edge-effect' in butterfly oviposition: causality in *Anthocaris cardamines* and related species. - Ecol. Entom. 7: 131-137.

GALL, L.F. 1987. Leaflet position influences caterpillar feeding and development. - Oikos 49: 172-176.

——. 1991a. Evolutionary ecology of sympatric *Catocala* moths (Lepidoptera: Noctuidae). I. Experiments on larval foodplant specificity. - J. Res. Lepid., 29: 173-194.

———. 1991b. Evolutionary ecology of sympatric *Catocala* moths (Lepidoptera: Noctuidae). II. Sampling for wild larvae on their foodplants. - J. Res. Lepid., 29: 195-216.

MILLER, W.A. 1977. *Catocala* (Noctuidae) species taken in Clay County, Tennessee. - J. Lepid. Soc. 31: 197-202.

NIELSON, M.C. 1978. Field Summary for 1977, Michigan report. - Lepid. Soc. News (May/June), p. 6.

ROWLEY, R.R., and L. BERRY. 1912. A dry year's yield of Catocalae (Lepid.). - Entom. News 23: 207-214.

SARGENT, T.D. 1976. Legion of Night: the Underwing Moths. - Univ. Mass. Press, Amherst. 222 pp.

SAS INSTITUTE INC. 1985a. SAS User's Guide: Basics, Version 5 Edition. - SAS Institute Inc., Cary, North Carolina. 1290 pp.

———. 1985b. SAS User's Guide: Statistics, Version 5 Edition. - SAS Institute Inc., Cary, North Carolina. 956 pp.

SCHWARZ, E. 1923. The reason why *Catocala* eggs are occasionally deposited on plants upon which the larva cannot survive; and a new variation (Lepid., Noctuidae). - Entom. News 34: 272-273.

SCHWEITZER, D.F. 1982. Field observations of foodplant overlap among sympatric *Catocala* feeding on Juglandaceae. - J. Lepid. Soc. 36: 256-263.

———. 1987. *Catocala pretiosa*, the precious underwing moth: results of a global status survey, with a recommendation for retention in category 2. - Status Survey Report to the US Fish & Wildlife Service, (Newton Corner, MA). 24 pp.

SOKAL, R.R., and F.J. ROHLF. 1982. Biometry (2nd Ed.). - Freeman, San Francisco. 859 pp.

STANTON, M.L. 1982. Searching in a patchy environment: foodplant selection by *Colias p. eriphyle* butterflies. - Ecology 63: 839-853.